

REVIEW OF *TOXOTHERIUM*  
(PERISSODACTYLA: RHINOCEROTOIDEA)  
WITH NEW MATERIAL FROM THE  
EARLY OLIGOCENE OF WYOMING

Robert J. Emry

*Abstract.*—Previously unreported specimens of the diminutive rhinocerotoid, *Toxotherium*, from the White River Formation (early Chadronian Age) of central Wyoming add new anatomical information and confirm some previous interpretations based on less nearly complete material. Occurring in a single thin stratigraphic interval are permanent lower dentitions referable to *Toxotherium hunteri*, deciduous lower dentitions referable to *T. woodi*, and upper dentitions referable to *Schizotheroides jackwilsoni*. The latter two species are placed in the synonymy of *T. hunteri*. *Toxotherium* is most likely an amynodontid.

---

Introduction

During the past ten years, several specimens of the rare, diminutive rhinocerotoid, *Toxotherium*, have accumulated as a result of collecting in the White River Formation of the Flagstaff Rim area in central Wyoming (Emry, 1973). Only four specimens of *Toxotherium* have been reported previously, each from a different locality, ranging from southern Saskatchewan to Trans-Pecos Texas. The new material includes maxillary dentition believed to represent *Toxotherium*, and also provides information suggesting that *T. woodi* is based on a juvenile *T. hunteri* and is therefore a synonym of *T. hunteri*. The upper dentition believed to be *T. hunteri* represents the same taxon as *Schizotheroides jackwilsoni* Schiebout, 1977, which is also placed in the synonymy of *T. hunteri*.

Abbreviations for the following institutional collections are used: AMNH, The American Museum of Natural History, New York; F:AM, Frick Collection, American Museum of Natural History; NMC, National Museum of Canada, Ottawa; SDSM, South Dakota School of Mines and Technology, Rapid City; TMM, Texas Memorial Museum, University of Texas, Austin; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Order Perissodactyla  
 Suborder Ceratomorpha  
 Superfamily Rhinocerotioidea  
 Family Incertae sedis  
 Genus *Toxotherium* Wood, 1961

*Toxotherium hunteri* Wood, 1961.

*Toxotherium woodi* Skinner and Gooris, 1966, new synonymy.

*Schizotheroides jackwilsoni* Schiebout, 1977, new synonymy.

*Type*.—NMC 8918, anterior half of right mandibular ramus with P<sub>4</sub>-M<sub>1</sub>.

*Hypodigm*.—Type and: F:AM 42901 (Type of *T. woodi*), partial left mandibular ramus with dP<sub>2</sub>(broken)-dP<sub>4</sub>, M<sub>1</sub>; TMM 40206-22, left M<sup>3</sup>; TMM 40840-42, maxillary fragment with right P<sup>4</sup>-M<sup>3</sup> (type of *Schizotheroides jackwilsoni*); TMM 40283-100, anterior part of right mandibular ramus with dP<sub>2-3</sub>; SDSM 8442, a partial left mandibular ramus with P<sub>4</sub>-M<sub>1</sub>; USNM 244352, left mandibular ramus with dP<sub>2-4</sub>, M<sub>1</sub>; USNM 244353, part of right M<sub>1</sub>; USNM 244354, right dP<sub>3</sub>; USNM 244355, left dP<sub>2</sub>; USNM 244356, left dP<sub>3</sub>; USNM 244357, left dP<sub>3</sub>; USNM 244358, right M<sup>1</sup>; USNM 244359, right maxillary fragment with M<sup>1-2</sup>; USNM 244360, posterior two-thirds of left M<sub>2</sub>; USNM 244361, left mandibular fragment with P<sub>4</sub>-M<sub>1</sub>; F:AM 79403, right dP<sub>4</sub>.

*Known distribution*.—Southern Saskatchewan, central Wyoming, eastern Wyoming, and Trans-Pecos Texas. The type of *Toxotherium hunteri* is from the Chadronian Cypress Hills Formation of Saskatchewan. *Toxotherium* was next reported from central Wyoming by Skinner and Gooris (1966), who described the new species *T. woodi*, which I believe on the basis of present evidence is juvenile *T. hunteri*, and which is from the lower part of the White River Formation, early Chadronian in age. *Toxotherium* was next recorded by Harris (1967) in the Ash Springs Local Fauna of the undifferentiated Vieja Group of the Sierra Vieja area of Trans-Pecos Texas, an occurrence also regarded as early Chadronian. Emry (1973) recorded *Toxotherium* in the fauna of the White River Formation in the Flagstaff Rim area of central Wyoming on the basis of a single tooth (F:AM 79403). SDSM 8442 is from the Yoder Local Fauna, early Chadronian, of Goshen Hole Wyoming (see Kihm, 1975). The two specimens described by Schiebout (1977) as *Schizotheroides jackwilsoni*, are, I believe, the upper dentitions of *Toxotherium hunteri*, for reasons explained below. All the other specimens listed in the hypodigm above (i.e., all the specimens with USNM numbers and F:AM 79403) are from the lower (early Chadronian) part of the White River Formation in the Flagstaff Rim area of central Wyoming. Of these, USNM 244352 through 244357 and F:AM 79403 came from a single rich concentration of bone that has many other mammalian taxa. This quarry is near the head of Little Lone Tree Gulch, at 44 feet below ash B on the

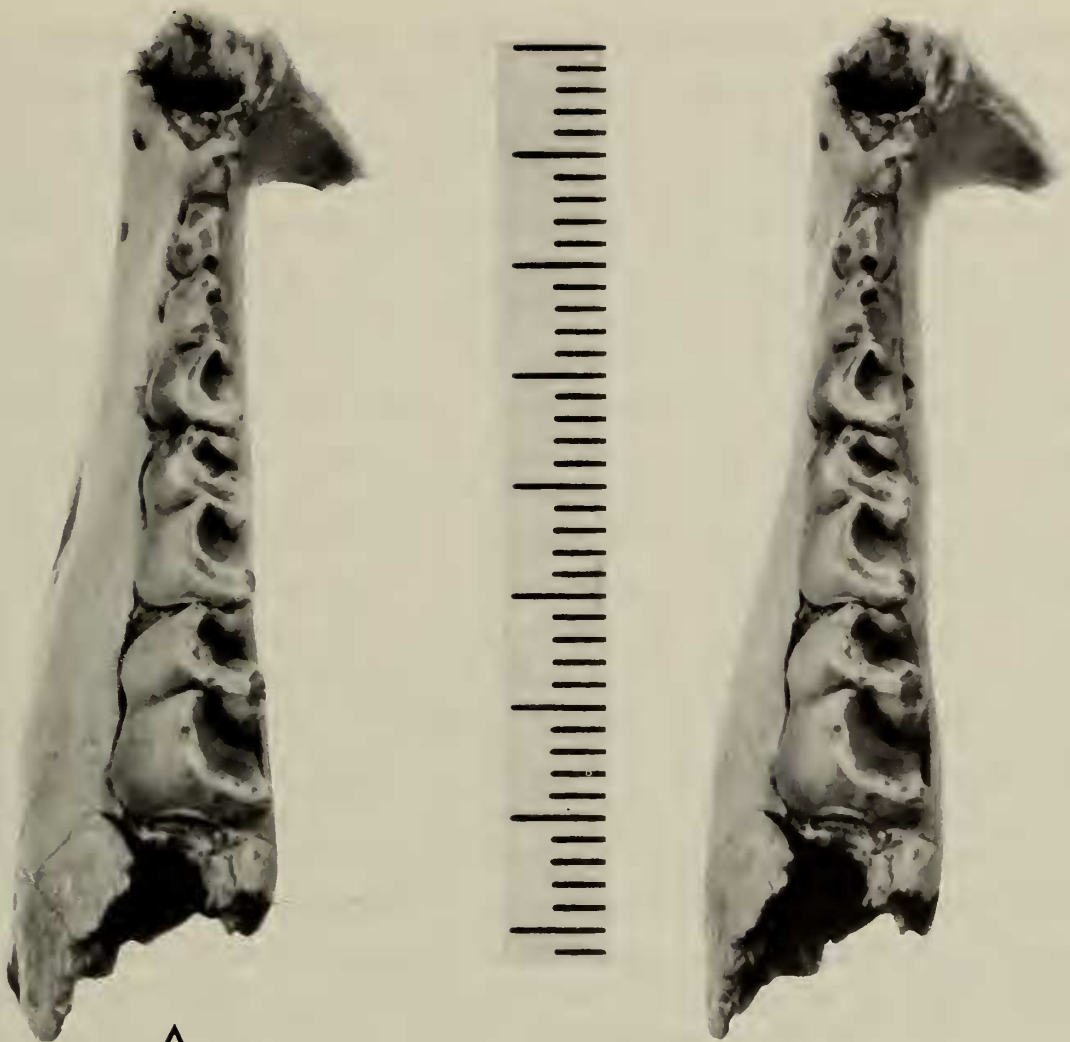
generalized zonation section of the Flagstaff Rim sequence (Emry, 1973, p. 29). The other specimens, USNM 244358 through 244361, came from a small area along the south side of Little Lone Tree Gulch, in the vicinity of the quarry, and within a relatively thin stratigraphic interval, the lowest occurrence at approximately 50 feet below ash B, and the highest at about 5–10 feet below ash B. The local range-zone for *Toxotherium* in the Flagstaff Rim section is from about 120 to 170 feet on the generalized section (Emry, 1973), although all but one specimen occurred in the much thinner interval between about 120 and 130 feet. The White River Formation here is more than 700 feet thick. The occurrence of *Toxotherium* only in this relatively restricted interval in a much thicker section suggests either that it had a very short temporal range, or that it preferred some particular environmental conditions that existed in the area only during the time in which this thin interval was being deposited.

All of the known occurrences of *Toxotherium* are Chadronian, and all for which more precise information is available (i.e., all except for the type of *T. hunteri*) are known to be early Chadronian. Although *Toxotherium* is now known from enough localities to define a rather large geographic range, it was apparently never an abundant element of any Chadronian fauna. Wood (1961) suggested that the late discovery of *Toxotherium*, and its apparent rarity, might be explained by its being a northern form, with the southern limit of its range near the Cypress Hills of southern Saskatchewan. The specimen from southern Saskatchewan now defines the northernmost limit of the known range, which extends southward as far as Trans-Pecos Texas.

*Associated fauna.*—The new material of *Toxotherium* is associated with a large number of vertebrate taxa, most of which are recognized as typical of Chadronian Age (though not necessarily restricted to the Chadronian), and some of which are indicative of early Chadronian. Among the taxa occurring in the quarry concentration with *Toxotherium* are the following: *Peratherium*, *Oligoryctes* cf. *O. altitalonidus*, Leptictid cf. “*Ictops*” *acutidens*, *Apternodus*, *Ischyromys* (or *Titanotheriomys*), *Protosciurus*, *Cylindrodon*, cf. *Yoderimys*, *Adjidaumo*, *Paradjidaumo*, ?*Namatomys*, *Aulolithomys*, *Heliscomys*, *Palaeolagus*, *Daphoenocyon*, *Hesperocyon*, ?*Parictis*, *Hyracodon*, *Merycoidodon*, *Agriochoerus*, *Poebrotherium*, *Hypisodus*, and the samples of *Leptomeryx* discussed by Emry (1973) as species B and D.

→

Fig. 1. *Toxotherium hunteri*, USNM 244352, left mandibular ramus of young individual with dP<sub>2-4</sub>, M<sub>1</sub>. A, occlusal view, stereogram, B, lateral view. Approximately ×2, scale in millimeters. Compare with F:AM 42901 (Skinner and Gooris, 1966, fig. 4, type of *T. woodi*), which is at same stage of ontogenetic development.



A



B

*Dental formula of Toxotherium.*—Wood (1961) identified the teeth present in the type of *T. hunteri* as  $P_{2-4}$ , with  $P_2$  preceded by alveoli for  $P_1$ . This interpretation was questioned by Skinner and Gooris (1966), who argued that the teeth present in the specimen are  $P_4-M_2$  with alveoli for  $P_3$ . Skinner and Gooris (1966) identified the most posterior tooth preserved in F:AM 42901 (type of *T. woodi*) as  $M_1$  because of its "abrupt increase in size and less wear on the crown relative to the preceding teeth." This interpretation is valid if the preceding teeth are correctly interpreted as deciduous premolars, an interpretation with which I agree, and for which additional evidence is found in the new material, particularly in USNM 244352 (Fig. 1). This jaw is virtually a duplicate of F:AM 42901, except that the most anterior tooth is complete rather than broken. The preservation is typical of the White River Formation, with pale tan to cream colored bone and brown teeth. In fossil mammals with this kind of preservation, and in which the deciduous dentition can be positively distinguished from the permanent, the color of the enamel of the deciduous dentition is usually distinctly lighter than that of the permanent teeth. The reason for this color difference has not been demonstrated, to my knowledge, although it is presumably related either to the relative thickness of the enamel (thinner in deciduous than in permanent teeth) or to some difference in its internal structure. In the *Toxotherium* jaw from Little Lone Tree Gulch, the anterior three teeth are distinctly lighter in color than the posterior one, indicating that the teeth are  $dP_{2-4}$ ,  $M_1$ , as Skinner and Gooris had determined for the type of *T. woodi*. The color difference is not apparent in Figure 1 because the specimen was given a light coat of ammonium chloride before it was photographed.

I interpret the teeth of the Vieja specimen (TMM 40283-100) as  $dP_{2-3}$ , rather than  $P_{3-4}$  as Harris (1967) believed them to be. Harris stated that the dimensions of the teeth of his specimen agree well with those of  $dP_{2-3}$  of *T. woodi*, and stated also that he was following the interpretation of Skinner and Gooris. The morphology of the more posterior of the two teeth is certainly more like that of  $dP_3$  of *T. woodi* than is it like that of the  $P_4$  of *T. hunteri*.

Too little is known about the maxilla of *Toxotherium* to allow even an educated guess as to the formula of the maxillary dentition. On the basis of present knowledge, the formula for the lower deciduous cheek teeth is  $dP_{2-4}$ , and for the permanent dentition is  $P_{3-4}$ ,  $M_{1-3}$ . This requires the assumption that  $dP_2$  is not replaced by a permanent  $P_2$ , but it is not unusual among mammals for the most anterior deciduous premolar not to be replaced, and this phenomenon seems to be more prevalent among groups undergoing reduction of the premolar series.

*The "tusk" of Toxotherium.*—Wood (1961), Skinner and Gooris (1966), Harris (1967), and Radinsky (1969), all commented on the large lower front tooth of *Toxotherium*, although in only one specimen (F:AM 42901, type of *T. woodi*) is even part of the tooth known. In the other specimens the

“disproportionately large” size of the tooth is an interpretation based on part of the outer wall and the basal part of its alveolus. Wood (1961), for example, as part of the diagnosis of *Toxotherium*, stated that it has a “single, disproportionately large, bulbous-rooted lower front tooth (incisor or canine).” The type of *T. woodi* has part of the tooth (called a tusk, to avoid the problem of homology) in place in the alveolus. Skinner and Gooris (1966) noted that the enamel of the tusk in their specimen “extends well back but not to the extreme base of the root,” and that the root is “open, a condition usually reflecting prolonged growth.” Any interpretation of the relative size of this tusk, however, must consider the age of the individual, which was very young (with the  $M_1$  erupted but essentially unworn, and  $M_2$  not yet erupted). I interpret the tusk of this specimen as an unerupted permanent caniniform tooth, with the root not yet formed. The “disproportionately large” size of the tooth can be accounted for, at least in part, by its being a permanent tooth only partly formed in an immature jaw.

Skinner and Gooris (1966) mentioned that the cross section of the “tusk” is about 41% of the ramal depth, but this comparison has little relevance. The depth of the jaw at this point is through the symphyseal area where the jaw is shallowest, and in this immature specimen the depth of the jaw at any point will be less than might be expected in a mature individual, whereas the diameter of the crown of the tusk would not increase once it had formed. A more significant comparison might be between the size of the tusk and the size of the cheek teeth. According to Skinner and Gooris, the greatest diameter of the “tusk at break” is 5.8 mm, or less than the anteroposterior dimension of  $dP_2$ , which is 6 mm. If the tusk is correctly interpreted as a permanent tooth, it would be even more meaningful to compare its size with that of a permanent cheek tooth. In this specimen (F:AM 42901) the only permanent cheek tooth present is  $M_1$ , which is 10 mm anteroposteriorly, according to Skinner and Gooris. The greatest cross-sectional diameter of the tusk is, then, 58% of the greatest dimension of  $M_1$ . The tusk does not seem disproportionately large in this context.

To determine how the tusk size, relative to  $M_1$ , of *Toxotherium* compares with that of other rhinocerotoids, a number of similar measurements were made on specimens in USNM collections. In the discussion following, tusk measurements are of the greatest cross-sectional dimension, and the  $M_1$  measurements are of the greatest anteroposterior dimension; all are in mm. In two specimens of *Trigonias* the tusks are 16.4 and 20.6, while the respective first molars are 34.5 and 32.2. In five specimens of *Subhyracodon*, the tusks are 19.7, 20.4, 20.0, 23.1, and 18.2, while the respective first molars are 29.9, 29.8, 29.6, 31.5, and 30.1. The tusk (second incisor in rhinocerotids) measurement averages 55% of the  $M_1$  measurement in *Trigonias* and 67% in *Subhyracodon*.

In two specimens of *Metamynodon* in the USNM collections, the tusks (which in amynodonts are canines) are 37.5 and 47.4 in their largest cross-

sectional dimension, while the respective first molars are 42.1 and 47.3. In these two specimens the tusk measurement averages 95% of the first molar measurement, though this statistic masks one instance in which the tusk measurement slightly exceeds the first molar measurement.

These statistics show that the tusk of *Toxotherium*, relative to the first molar, is not disproportionately large when compared to those of other rhinocerotoids. It is relatively slightly larger than that of *Trigonias*, somewhat smaller than that of *Subhyracodon*, and much smaller than that of *Metamynodon*. In terms of tusk size, *Toxotherium* is not an unusual rhinocerotoid.

*Identity of Toxotherium woodi.*—In the introduction of their paper describing *Toxotherium woodi*, Skinner and Gooris (1966) stated that "certain characters separate the Bates Hole specimen, specifically at least, from *T. hunteri*." They did not provide a diagnosis for the species, however, and no distinguishing characters were specifically mentioned elsewhere in the text except for the statement (1966:9) that in *T. woodi* the dental series is "shortened by the loss of  $P_1$ , not by both  $P_1$  and  $P_2$  as in *T. hunteri*." This conclusion assumes that the deciduous  $P_2$  of *T. woodi* is replaced by a permanent  $P_2$ , an assumption for which there is no evidence. The material discovered since that time does not clarify this question. The permanent dentitions known either have no  $P_2$ , or are too incomplete to determine whether or not  $P_2$  was present. All the juvenile specimens with anterior premolars preserved have  $dP_2$ .

The type of *T. hunteri* is a jaw of an individual that was still young but approaching maturity, with  $M_2$  slightly worn and  $M_3$  not yet erupted. The type of *T. woodi* represents a much younger individual, with the deciduous premolars still in place,  $M_1$  practically unworn, and  $M_2$  not yet erupted. Dental comparisons between the two specimens are therefore limited to  $M_1$ , which, as noted by Skinner and Gooris (1966), are morphologically similar and very nearly the same size in the two specimens. While *T. hunteri* appears to be considerably larger, the size difference is surely related to different ontogenetic development; dentally the size difference is insignificant (Table 1).

The new material from central Wyoming provides additional information suggesting that *T. woodi* represents a young individual of *T. hunteri*. USNM 244352 (Fig. 1) is virtually a duplicate of the type of *T. woodi*, except that  $dP_2$  is more nearly complete. The other deciduous teeth from the same quarry (see hypodigm above) are morphologically like those of the type of *T. woodi*. There would be no hesitation in assigning all the juvenile specimens to *T. woodi*, were it not for the fact that in the very same thin stratigraphic interval in the same very restricted area, specimens with permanent dentition occur that could be assigned without hesitation to *T. hunteri*. USNM 244361 (Fig. 2), a jaw fragment bearing  $P_4$ - $M_1$ , compares very well

Table 1. Measurements, in millimeters, of teeth of *Toxotherium hunteri*.

Specimen number	Tooth	Maximum length, anteroposterior	Maximum width, transverse
TMM 40206-22	M <sup>3</sup>	16.3	18.1
TMM 40840-42	P <sup>4</sup>	9.4 (minimum)	11.8
	M <sup>1</sup>	13.7	13.9
	M <sup>2</sup>	18.2	17.5 (estimate)
	M <sup>3</sup>	17.2	20.2
USNM 244359	M <sup>1</sup>	12.3	12.2
	M <sup>2</sup>	14.8	15.0 (estimate)
USNM 244358	M <sup>1</sup>	11.5	12.1
NMC 8918 (type)	P <sub>4</sub> -M <sub>2</sub>	32.6	
	P <sub>4</sub>	8.3	5.6
	M <sub>1</sub>	10.3	6.1
	M <sub>2</sub>	14.1	8.0
F:AM 42901	dP <sub>3</sub> -M <sub>1</sub>	26.6	
	dP <sub>3</sub>	7.8	4.6
	dP <sub>4</sub>	8.8	5.1
	M <sub>1</sub>	10.0	6.3
USNM 244352	dP <sub>2</sub> -M <sub>1</sub>	28.2	
	dP <sub>3</sub> -M <sub>1</sub>	25.2	
	dP <sub>2</sub>	3.6	2.3
	dP <sub>3</sub>	7.2	4.2
	dP <sub>4</sub>	8.3	5.1
	M <sub>1</sub>	9.9	6.2
USNM 244361	P <sub>4</sub>	7.8	5.6
	M <sub>1</sub>	9.4	6.2
TMM 40283-100	dP <sub>2</sub>	5.0	3.0
	dP <sub>3</sub>	7.8	4.5
SDSM 8442	P <sub>4</sub>	8.3	5.5
	M <sub>1</sub>	10.2	6.4
USNM 244355	dP <sub>2</sub>	4.3	2.7
USNM 244354	dP <sub>3</sub>	6.2	3.8
USNM 244356	dP <sub>3</sub>	7.6	4.0
USNM 244357	dP <sub>3</sub>	7.5	4.2
F:AM 79403	dP <sub>4</sub>	8.6	4.8
USNM 244353	M <sub>1</sub>		6.1
USNM 244360	M <sub>2</sub>		7.9

with the type of *T. hunteri*; it is slightly smaller but certainly within the range of variation that might be expected in a single species. The depth of the jaw of this specimen cannot be determined because the lower border is not preserved, but even the fragment remaining is much deeper than the entire jaw below M<sub>1</sub> of USNM 244352 (Fig. 1) which has a slightly larger M<sub>1</sub> but is a much younger individual. The maxillary fragment with M<sup>1-2</sup> (USNM 244359, Fig. 3) at first appears to be too large to be *Toxotherium*, but when it is occluded with the type of *T. hunteri* (the only lower jaw of



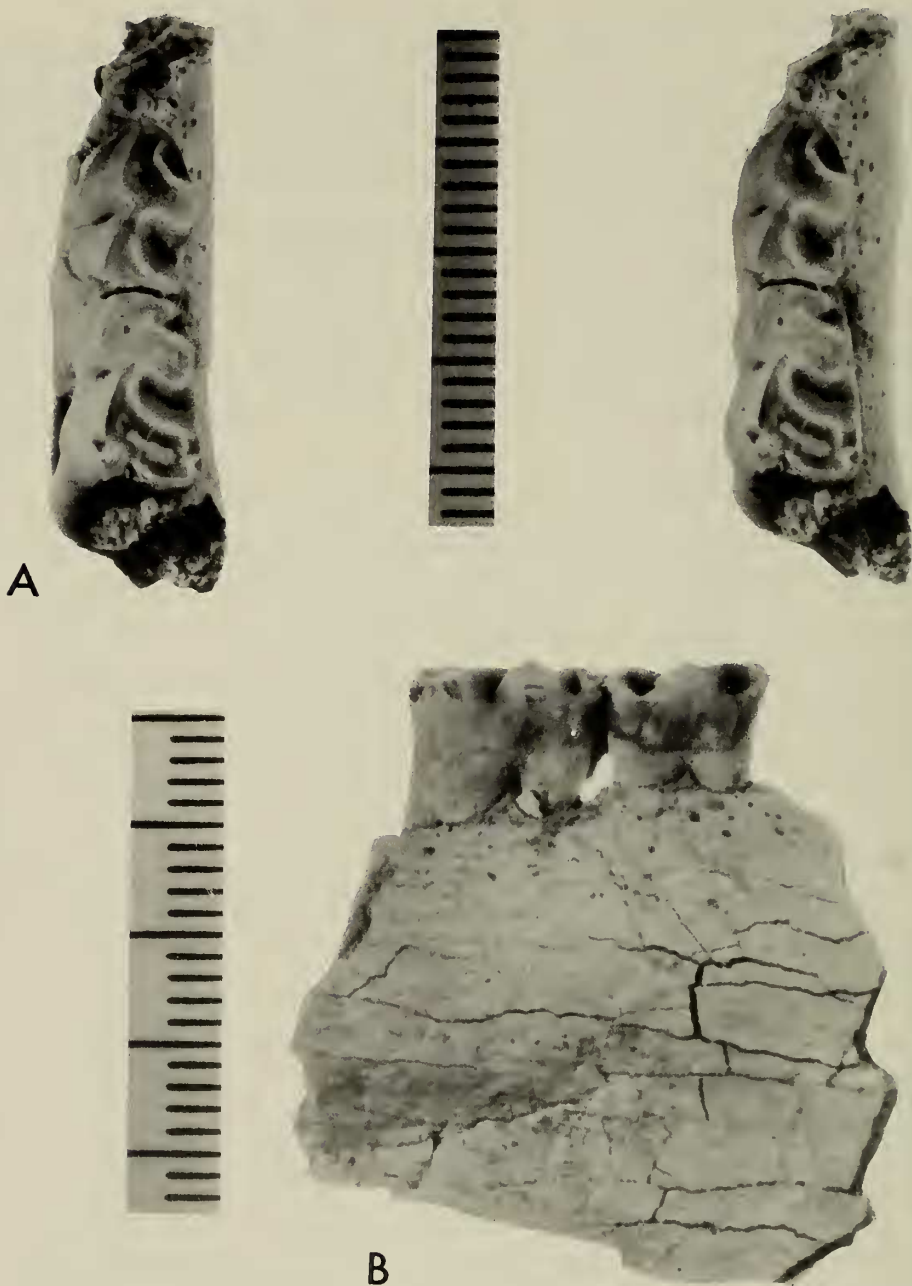


Fig. 2. *Toxotherium hunteri*, USNM 244361, left mandibular fragment with  $P_4$ - $M_1$ . A, occlusal view, stereogram; B, lateral view. Approximately  $\times 2$ , scale in millimeters. Compare with NMC 8918 (Wood, 1961, figs. 1-3, type of *T. hunteri*).

*Toxotherium* with an  $M_1$  and  $M_2$  to occlude) it is seen to be precisely the right size. The wear facets of the upper teeth all occlude correctly with those of the lowers. These upper teeth, and an isolated  $M^1$  (USNM 244358), were found in the same thin stratigraphic interval in which the lower teeth and jaws of *Toxotherium* occur. Neither upper dentitions like those mentioned nor lowers of *Toxotherium* occur elsewhere in the more than 700 feet of White River section. In the interval in which they occur, there are no other upper dentitions that could conceivably be associated with *Toxotherium* and no other lower dentitions that could conceivably be associated with these upper dentitions. Though the association is circumstantial, I think

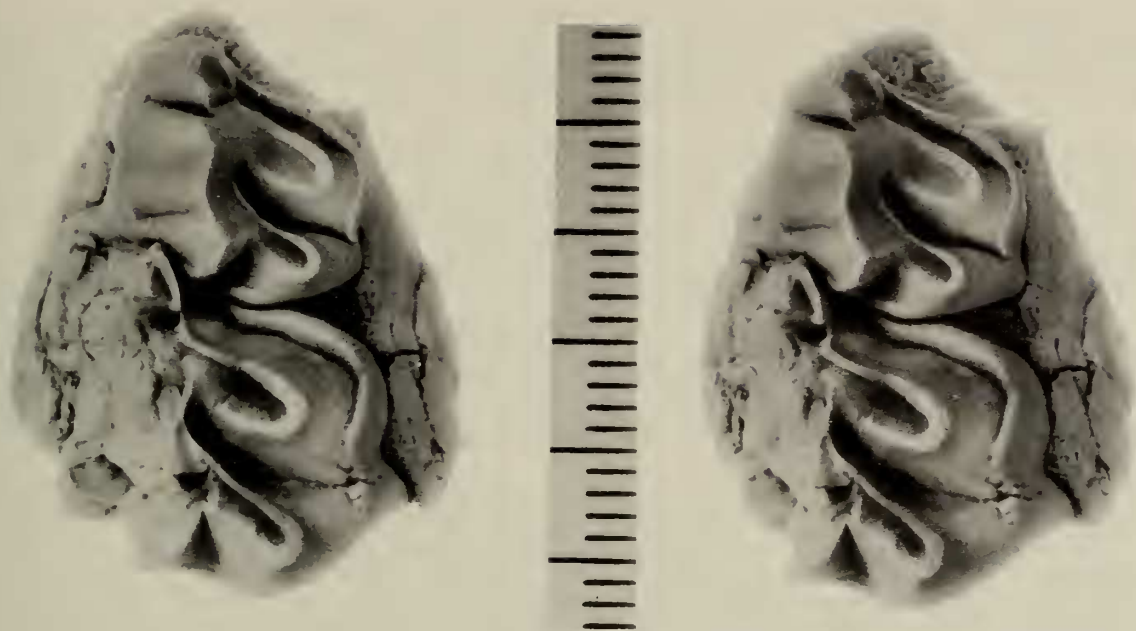


Fig. 3. *Toxotherium hunteri*, USNM 244359, right maxillary fragment with M<sup>1</sup> and most of M<sup>2</sup>, stereogram. Approximately  $\times 2$ , scale in millimeters. Compare with TMM 40840-42 (Schiebout, 1977, fig. 1f, type of *Schizotheroides jackwilsoni*).

the evidence is quite persuasive that these upper dentitions are of *Toxotherium*.

The lack of any morphological features to separate *T. hunteri* and *T. woodi*, and the association of specimens assignable to both species in the same deposits, leads to the conclusion that *T. woodi* merely represents very young individuals of *T. hunteri*. I therefore place *T. woodi* in the synonymy of *T. hunteri*.

*Identity of Schizotheroides jackwilsoni*.—Skinner and Gooris (1966) discounted the idea that *Toxotherium* might represent the lower dentition of *Schizotheroides* Hough (1955), an enigmatic perissodactyl known only from the late Eocene of Sage Creek, Montana. Their reasons were that the cusp pattern of *Schizotheroides* is not as distinctly rhinocerotoid as that of *Toxotherium*, and they believed that upper dentition with heavy cingula, as in *Schizotheroides*, was not likely to be combined with lower dentition with very weak, or no, cingula, as in *Toxotherium*. Schiebout (1977), in her description of what she regarded as a new species of *Schizotheroides*, cited the reasons given by Skinner and Gooris for not associating *Schizotheroides* and *Toxotherium*. Here the problem begins, because the material on which Schiebout based *Schizotheroides jackwilsoni* certainly represents the same taxon as the upper dentitions from Little Lone Tree Gulch (USNM 244358 and 244359), which I believe, for reasons discussed above, represent the upper dentition of *Toxotherium hunteri*. I believe that the Vieja specimens are also *Toxotherium*, but not that *Toxotherium* is a synonym of *Schizotheroides*.

The two specimens from the Vieja Group occur in local faunas in which

lower dentitions of *Toxotherium* have not been found, but *Toxotherium* is recorded (Harris, 1967) in the Vieja Group in the nearby Ash Springs Local Fauna. As in the White River Formation, there are no other upper dentitions that could be associated with *Toxotherium*, and no other lower dentitions that could be associated with *Schizotheroides jackwilsoni*.

Though the association can be proven only by finding upper dentitions articulated, or directly associated, with lowers, I believe the present evidence is persuasive. As pointed out above, the association of upper and lower dentitions in the Flagstaff Rim sequence is even more compelling. I therefore place *Schizotheroides jackwilsoni* in the synonymy of *Toxotherium hunteri*.

As Schiebout (1977, p. 456) mentioned, *S. jackwilsoni* is larger and more hypsodont than *S. parvus*, the genotypic species, and in *S. jackwilsoni* the third molar is both longer and wider than the second, whereas the opposite is true of *S. parvus*. There are other differences not mentioned by Schiebout. In *S. parvus*, the protoloph turn posteriorly at the lingual ends, most noticeably on  $M^3$ , so that these lophs are concave posteriorly when seen in occlusal view, in contrast to those of the Vieja and Little Lone Tree Gulch specimens in which the protoloph and metalophs are concave anteriorly, particularly on  $M^1$  and  $M^2$ . *S. parvus* has a continuous cingulum from the parastyle across the anterior, lingual, and posterior border, to the posterior end of the metacone, on both  $M^2$  and  $M^3$  (Schiebout's illustration of *S. parvus* does not show a cingulum around the lingual end of the protoloph of  $M^3$ , but it is present on the specimen, and shows clearly in Hough's original illustration, 1955, pl. 8, fig. 1). *S. parvus* has a distinct labial cingulum, more prominent on  $M^2$  than on  $M^3$ , and on  $M^3$  a small but distinct mesostyle. This is in contrast to the Vieja and Little Lone Tree Gulch specimens which have a distinct anterior cingulum which ends at the lingual end of the protoloph, no labial or lingual cingula on  $M^1$  and  $M^2$ , and a very short and weak posterior cingulum, barely indicated on  $M^1$  and  $M^2$ . The third molars illustrated by Schiebout (1977, fig. 1d-f) have weak lingual cingula, and one has a faint suggestion of a labial cingulum. None has a mesostyle.

Schiebout's illustration of *S. parvus* (1977, fig. 1a-b) is inaccurate in several details which are clearly shown in Hough's original photographic illustration of the specimen (1955, pl. 8, fig. 1). The cingulum of  $M^3$  was mentioned above. Schiebout's illustration shows no hint of a protoconule, which is quite distinct in the specimen, particularly on  $M^3$ , and in Hough's photograph. The paracone is much more distinct than shown by Schiebout; the protocone, particularly of  $M^3$ , turns posteriorly much more than indicated by Schiebout; and the valley separating the paracone and parastyle is incorrectly placed in Schiebout's drawing. This valley, which is shown by Schiebout as intersecting the ectoloph posterior to the protoloph-ecto-

loph junction, is actually at the junction, opposite the valley separating the protoloph and parastyle, so that the ectoloph, protoloph, and parastyle meet at a common point.

The large parastyle of  $M^3$ , with its crest oriented anterolabially-posterolingually, is the one unusual feature common to *Schizotheroides parvus* and the upper dentition here referred to *Toxotherium hunteri*. While this may suggest some relationship between the two taxa, the many differences pointed out above are, in my opinion, sufficient to separate them at least at the generic level. Not enough is known, particularly of *S. parvus*, to make a good case either for or against a relationship. *Toxotherium hunteri* is certainly more derived than *S. parvus* in a number of features, such as complete merging of the protoconule into the protoloph, increased hypsodonty, and loss of lingual, labial, and most of the posterior cingula of the molars.

*Discussion.*—*Toxotherium* has resisted placement in a taxonomic category lower than superfamily. Wood (1961) was apparently confident that it belongs to the Suborder Ceratomorpha, and believed that it is probably assignable to the Superfamily Rhinoceroidea. Skinner and Gooris (1966) assigned *Toxotherium* to the Rhinoceroidea, as have the other authors who have since mentioned it. Radinsky (1969) noted that *Toxotherium* has a rhinocerotoid molar pattern, and an enlarged, procumbent tusk, and suggested that it may be an aberrant, diminutive amynodontid. The new material of *Toxotherium* does little to resolve the matter, but the additional information is more suggestive of amynodont affinities than any other alternative.

Amyndonts typically have massive skulls and jaws, with the facial part of the skull relatively short for a perissodactyl. *Toxotherium* was very small, but relative to the size of its teeth the dentary was massive, and the relatively wide angle between the lower jaws (mentioned by Skinner and Gooris, 1966, and Harris, 1967) suggests that *Toxotherium* was brachycephalic. Other trends in amynodonts (Radinsky, 1969) are reduction of the premolar series, increasing hypsodonty and relative narrowing of the molars, with some increase in obliquity of the cross crests. These trends are also manifest in *Toxotherium*, which has lost both  $P_1$  and  $P_2$  of its permanent dentition. The teeth are relatively high crowned for a rhinocerotoid with so little molarization of the premolars, a condition noted by Wood (1961), and the cross crests of the molars are somewhat more oblique than in rhinocerotids and much more oblique than in tapiroids. In the upper dentition (Fig. 3, and Schiebout 1977, figure 1f), the cross lophs are also oriented at an oblique angle to the ectoloph.

The upper dentition assigned here to *Toxotherium* would be somewhat contradictory as an amynodont because of the large parastyle of  $M^3$ . Typical amynodonts have parastyles that are considerably smaller, more columnar, and not deflected anterobuccally. But this parastyle is unusual for any pe-

rissodactyl and would be a contradictory feature in assigning *Toxotherium* to any family. Schiebout (1977) did point out that, despite the unusual form of the parastyle in the Vieja specimens, it nevertheless functions just as it does in the hyracodontid rhinocerotoid *Triplopus*, by forming, along with the posterior end of the ectoloph of the next anterior tooth, a surface which shears against the labial side of the protoconid.

Because the evidence is so limited and in part contradictory, it seems best for the present to defer assigning *Toxotherium* to a family, and simply to leave it in *Rhinoceroidea incertae sedis*.

*Schizotheroides*, like *Toxotherium*, has resisted assignment to suprageneric categories. Hough (1955) placed it questionably in the Superfamily Chalicotheroidea. Radinsky (1964) noted that the parastyle of *Schizotheroides parvus* is more compressed anterolingually-posterolabially than in chalicotheres, and that "the only other features at all suggestive of chalicotheres are a slight swelling midway down the posterior side of the worn M<sup>2</sup> protoloph, and, also on M<sup>2</sup>, a sharp cingular cuspule between paracone and metacone (which is probably merely an abnormal variation, but may indicate incipient mesostyle development)." Radinsky regarded the absence of a distinct protoconule as a strong argument against placing *Schizotheroides* in the Chalicotheroidea (1964). Although I agree with Radinsky that *Schizotheroides* is not a chalicotheroid, it should be pointed out that *Schizotheroides* does have more distinct protoconules than Radinsky's comments would suggest. It seems incongruous that Radinsky mentioned the trace of a protoconule on the worn M<sup>2</sup>, but did not mention that M<sup>3</sup> has a protoconule even more distinct. Neither did Hough mention the presence of a protoconule in *Schizotheroides parvus*, though it is distinctly evident in the illustration accompanying her type description (Hough 1955, pl. 8, fig. 1). The protoconules of *Schizotheroides parvus* are more distinct than in any of the many *Homogalax* specimens in the USNM collections. Radinsky (1969) noted that a characteristic of tapiroids is the complete lack of protoconules in the molars, except in *Homogalax*, the earliest known tapiroid, which retains traces of protoconules. If the absence of protoconules is characteristic of any tapiroid later than *Homogalax*, then *Schizotheroides* is excluded from the Tapiroidea, since it has more distinct protoconules and occurs later than *Homogalax*.

It is not an objective of this report to classify *Schizotheroides*; more material of *S. parvus* is needed before the question of its affinities can be answered. I will follow Radinsky (1964) in leaving it in *Perissodactyla incertae sedis*.

#### Acknowledgments

Some of the most nearly complete specimens mentioned in this report were found by volunteer field assistants, who deserve special mention; the

jaw shown in Fig. 1 was found by Elizabeth Hunter and that shown in Fig. 2 was found by Jennifer Emry. The manuscript was read by John A. Wilson, Morris F. Skinner, Shirley M. Skinner, Clayton Ray, and Donald Prothero; I thank them for improvements resulting from their comments and corrections.

### Literature Cited

- Emry, R. J. 1973. Stratigraphy and preliminary biostratigraphy of the Flagstaff Rim area, Natrona County, Wyoming.—*Smithsonian Contr. to Paleobiol.* 18:1–43.
- Harris, J. M. 1967. *Toxotherium* (Mammalia: Rhinoceroidea) from western Jeff Davis County, Texas.—*Pearce-Sellards Series* 9:1–7.
- Hough, J. 1955. An upper Eocene fauna from the Sage Creek area, Beaverhead County, Montana.—*Jour. Paleont.* 29:22–36, pls. 7–8.
- Kihm, A. J. 1975. Mammalian paleontology of the Yoder Local Fauna.—Unpublished masters thesis, South Dakota School of Mines and Technology, Rapid City, S. D.
- Radinsky, L. B. 1964. *Paleomoropus*, a new early Eocene chalicothere (Mammalia, Perissodactyla), and a revision of Eocene chalicotheres.—*Amer. Mus. Novitates* 2179:1–28.
- . 1969. The early evolution of the Perissodactyla.—*Evolution* 23:308–328.
- Schiebout, J. A. 1977. *Schizotheroides* (Mammalia: Perissodactyla) from the Oligocene of Trans-Pecos Texas.—*Jour. Paleont.* 51:455–458.
- Skinner, S. M., and R. J. Gooris. 1966. A note on *Toxotherium* (Mammalia, Rhinoceroidea) from Natrona County, Wyoming.—*Amer. Mus. Novitates* 2261:1–12.
- Wood, H. E., II. 1961. *Toxotherium hunteri*, a peculiar new Oligocene mammal from Saskatchewan.—*Nat. Hist. Papers, Natl. Mus. Canada* 13:1–4.

Department of Paleobiology, National Museum of Natural History,  
Smithsonian Institution, Washington, D.C. 20560.